

TRANSACTIONS OF  
THE ROYAL SOCIETY  
OF CANADA

SECTION V  
BIOLOGICAL SCIENCES



THIRD SERIES—VOLUME LIII—SECTION V  
JUNE, 1959

OTTAWA  
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# TRANSACTIONS OF THE ROYAL SOCIETY OF CANADA

VOLUME LIII : SERIES III : JUNE, 1959

## SECTION FIVE



### The Origin of the Metazoa

J. R. NURSALL

Presented by R. F. SHANER, F.R.S.C.

THE consensus of biologists nowadays is that life could have originated from several combinations of inorganic materials under the influence of one or several of a variety of phenomena. Many recent works outlining possible modes of origin are readily available (for example, 4; 5; 14; 17; 20; 22). By and large it is agreed that life began during time when free oxygen was not present in the atmosphere. Any oxygen that did appear was immediately taken up in inorganic oxidations. Clearly life existed anaerobically for a great period of time.

The origin of life can be thought of as a single occurrence which became repetitive, presumably autocatalytically; or as a self-reproducing reaction which recurred many times, perhaps over a long period of time; or as a number of reactions related to each other in a number of ways, each also probably newly occurring over a long period of time; or even as a number of entirely unrelated reactions (for example, thermal or ultraviolet radiative or adsorptive phenomena, etc.) each perhaps occurring repeatedly during the course of thousands of years.

Whatever the origin, at least two things must be assumed: first that a supply of organic matter was present as nutrient to these first shadows or life or eobionts (19), and second that the eobionts could utilize the nutrient by adsorption or absorption. It is, of course, possible that the original forms of life were autotrophic and so could create their own organic matter, but this seems to presuppose rather greater chemical organization than one might like to allow so early. Furthermore, it has been abundantly shown that organic matter could have been originated by physico-chemical means from the inorganic compounds which undoubtedly were present. It seems best to say that organic matter came first and that the first living things were heterotrophic, that is, they extracted their organic nourishment from their environment.

We still must consider the form of the origin of life. If we accept a single primordial reaction as the source of life we certainly simplify the scheme of things. We also accept an occurrence of impressive improbability which can, however, be argued around, as Simpson (23) has shown in another context. By presenting reasonable conditions for a long enough time one can reduce the apparently impossible to near certainty. What is worse than its improbability is the unnaturalness of the scheme. Nature, whose cognition

is slight, is not apt to try something once and then exclude all else when she sees it is good. Even if a single type of reaction represented the moment of origin, it is likely that the reaction was repeated time after time. If the reaction were autocatalytic and if it continued to originate (*de novo*) through a long period of time and if it had that characteristic of life called variability, the progeny or reaction products several generations descended from the first occurrence would have been changed from the first product of the last reaction. There would be two types of things originated and probably more!

This divergence of beings would be accentuated if all the new reactions were not the same. As soon as differences began to appear, affected eobionts would have new requirements, some of which would kill their possessors, others which would give their owners distinct advantages within the environment.

If there were a long period of origination and establishment of types one would expect at first an increase in numbers of forms. When new types ceased to originate there would follow a long period of reduction of numbers of types as the less and more successful sorted themselves out and died or flourished respectively. Direct competition for the needs of life need not have been of much importance at this early stage. Success or failure would tend to be more personal, the radical organism living dangerously in a conservative environment. Heterotrophic nutrition is remarkably complex as Oparin (17, p. 403 *et seq.*) has pointed out. The organism, to survive, must stay within the limits of environmental provender and its own ability at synthesis.

Autotrophes have been suggested as derivatives of the preceding heterotrophes (16). When this step was attained, relative independence of dissolved environmental organic matter was possible. Indeed, it is likely that the photosynthetic autotrophes (soon to be algae) became the dominant organisms. However, they undoubtedly supported numbers of heterotrophes, probably of several types, in a manner analogous to autotrophic support of heterotrophes today.

Algae flourished for millions of years. Their traces have been found in ancient rocks from around the world. It was these algae that provided the surplus of free oxygen which is now a major component of the atmosphere and hydrosphere. It must have been a long time before inorganic reactions no longer removed oxygen as soon as it appeared. Under the influence of free oxygen there came a rapid evolution of animal and plant forms (16; 17; 21).

There evolved in a very short period, a few millions of years, Metazoa. That Metazoa appeared with some suddenness is attested by the fossil record. The lower levels of the Cambrian, first period of the Palaeozoic, are marked by trilobites, which are complex arthropods. It is generally believed that all phyla of animals, and probably plants, were represented by the end of the Cambrian period.

It is relatively simple to picture the evolution of plants continuing from the autotrophic algae. It is less easy to reconstruct the course of evolution of animals. Most attempts start with Protozoa, which is assumed to be a group of single ancestry. From Protozoa the trail leads to Coelenterata, usually by means of a colonial form. Baker (1) pointed out the likelihood that Metazoa had arisen from Protozoa because of failure of separation of cells after division. As an instance of a more detailed study of this sort of course of events, Hyman (13) showed how developmental similarities between volvocines and sponges suggest a relationship. She then attempted to extend this relationship to the coelenterates. Hardy (11) suggested that metazoans might have arisen from primitive metaphytes, which he likened to volvocines. Further, in most phylogenies, Platyhelminthes are derived from Coelenterata, and so on. Much ingenuity is exercised in drawing phylogenetic trees to show the relationships of all phyla. The chief leafy decoration of these trees, however, is question marks.

Hadži (9) made a strong effort to break away from the Haeckelian scheme outlined above. He suggested that acoel platyhelminths were the first metazoans. From these there evolved, in a straight-line series, the rest of the animal kingdom. The first part of this theory has recently been taken up in detail by Hanson (10) who suggests certain holotrichous ciliates as representative of a group which could have been ancestral to the acoels. Carter (6) criticized Hadži's straight-line evolution and concluded "that the invertebrate phyla arose, many more or less simultaneously, in the course of radiations of very early metazoan stocks, perhaps a single stock, perhaps two or more." Carter strongly maintained that most metazoans can be divided naturally into Protostomia or Deuterostomia, even if all arose from a single stock.

Whittaker (24) argued that at least three major evolutionary tendencies have occurred in the development of living matter. The three are exemplified by plants, animals, and saprobes (primarily fungi), or put another way, by photosynthetic organisms, ingestive organisms, and absorbing organisms. These he would rank as kingdoms, all derived from unicellular organisms. In the three groups there are two types of heterotrophes and one autotrophic type.

The idea of evolutionary tendencies is important. It is to be remembered that evolution is neither directed nor random, but is, in effect, channelled. A certain form can be modified only in certain ways to survive under certain conditions. That which will evolve depends upon that which has evolved. In this connection the ideas of Pantin (2; 18) are well worth considering. He has pointed out that organisms are built up of standard parts which have unique properties. He analogized the standard parts to pieces of a child's construction set which can be assembled in many ways, but the constructions always have similarities and limitations imposed upon them by the nature of the building pieces. In his presidential address to Section D of the British Association in 1951, Pantin dwelt at some length

on the molecular level of structure and pointed out how the molecular level determines the gross. A limited variety of molecular reactions can be utilized in many ingenious ways by organisms, for instance, polyphenolic linkages of fibrous proteins to form insect exoskeletons, eggshells of liver flukes, silk, mollusc anchoring threads, stickleback nest binding. In a sense this is Henderson's (12) environmental fitness brought up to date. Organisms exist because of what is present in the environment and they survive because there is community of matter and reaction between them.

A more formal statement of a similar point of view comes from Novikoff (15). Novikoff calls the regularity of form in organisms homomorphism, which "is probably a reflection of the inability of living matter to form efficient organs of specified function (photoreception, for example) in more than a limited number of ways."

These conclusions lead one to believe that there might be found a great deal of convergent similarity in organisms because there is a limited number of ways cells and tissues can be used in dealing with the exigencies of existence. It is possible, to state it in simple fashion, that the fact that most organisms consist of mitotic cells might not indicate common organismic ancestry but rather it might indicate convergent use of limited ways and means of survival and evolution. Boyden (3) has dealt at length with this particular problem.

If there were a number of different types of eobionts during pre-organismic life, following a number of evolutionary tendencies using limited means, it could be that the phyla of animals as we classify them now might represent three or four separate groups, each independently evolved from a distinct ancestral eobiont type. I think we might consider seriously the possibility that groups of phyla originated independently and that each of these has evolved its own types in radiations from successive levels of organization. I do not now propose to outline possible groupings of phyla, but I suggest that perhaps one should look for differences rather than similarities wherever particular difficulty arises in joining disparate groups.

Darwin himself considered this problem in a general way, and apparently failed to resolve it to his satisfaction. In the first edition of the *Origin of Species* (7, p. 410) he said, "I believe that animals have descended from at most only four or five progenitors, and plants from an equal or lesser number." But continuing, he concludes "I should infer from analogy that probably all organic beings which have ever lived on this earth have descended from some one primordial form, into which life was first breathed." In the sixth edition (8, p. 370) the concluding statement is greatly modified, as follows: "all organic beings which have ever lived on this earth may be descended from some one primordial form. But this inference is chiefly grounded on analogy and it is immaterial whether or not it be accepted. No doubt it is possible, as Mr. G. H. Lewes has urged, that at the first commencement of life many different forms were evolved; but if so we may conclude that a very few have left modified descendants. For, as I have

recently remarked in regard to the members of each great kingdom, such as the Vertebrata, Articulata, etc., we have distinct evidence in their embryological, homologous and rudimentary structures that within each kingdom all the members are descended from a single progenitor."

What is suggested here is not new, nor is it liable to be agreed upon quickly if correct. But I think it is worth investigating, for if it is true it will lead to new understanding of the phenomena of living matter and save the time of those who would string tenuous threads of relationship from phylum to phylum.

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The Evolution of the Chondrophora (Siphonophora-  
Disconanthae): New Evidence from  
Behavioural Studies

G. O. MACKIE

Presented by R. G. H. CORMACK, F.R.S.C.

INTRODUCTION

THE problem of siphonophore evolution and relationships has long given grounds for controversy. The primary schism arose in the last century between those such as T. H. Huxley, Metschnikoff, Haeckel, and Hatschek who regarded the siphonophores as modified medusoid organisms giving rise by budding from the sub-umbrella to secondary medusae and polyps and, on the other hand, those such as Leuckart, Vogt, A. Agassiz, and Chun who regarded them as floating colonies of hydroid-polyps, showing specialization and division of labour, and budding off medusae. Within these two camps endless shades of opinion existed, as Leloup (12) has described. In the present century both views have continued to find adherents. Among the leading specialists, however, only Moser has supported the medusoid theory. In the special case of the Chondrophora, Leloup's demonstration (11) of the actinuloid nature of the conaria larva of *Vellela* and Garstang's detailed analysis (7) of the corymorphine affinities of the group have been influential in establishing the Chondrophora (*a*) as polypoid organisms and (*b*) as a fundamentally distinct group, possibly representing a line of evolution separate from that of the true siphonophores. In Totton's authoritative classification (20) the Chondrophora are established as a separate order within the Hydrazoa.

In spite of these advances, forms such as *Vellela* and *Porpita* continue to be treated together with the true siphonophores and are, indeed, often thought to be typical members of the group. Furthermore, in the majority of modern accounts the medusoid hypothesis continues to hold sway, the float (pneumatophore) being viewed as a modified medusa from beneath which the polypoid members are budded. A noteworthy exception is Hardy (9) who follows Garstang's interpretation.

Since the present paper provides evidence supporting the tubulariid affinities of the Chondrophora, a brief comparison of the gross morphology and development of the two groups is a necessary preliminary.

CHONDROPHORE STRUCTURE AND HOMOLOGIES

*Porpita* hangs at the surface with the oral aperture (Fig. 1 D, *o*; Plate I) facing down. The upper portion of the disc is above water level. The mantle

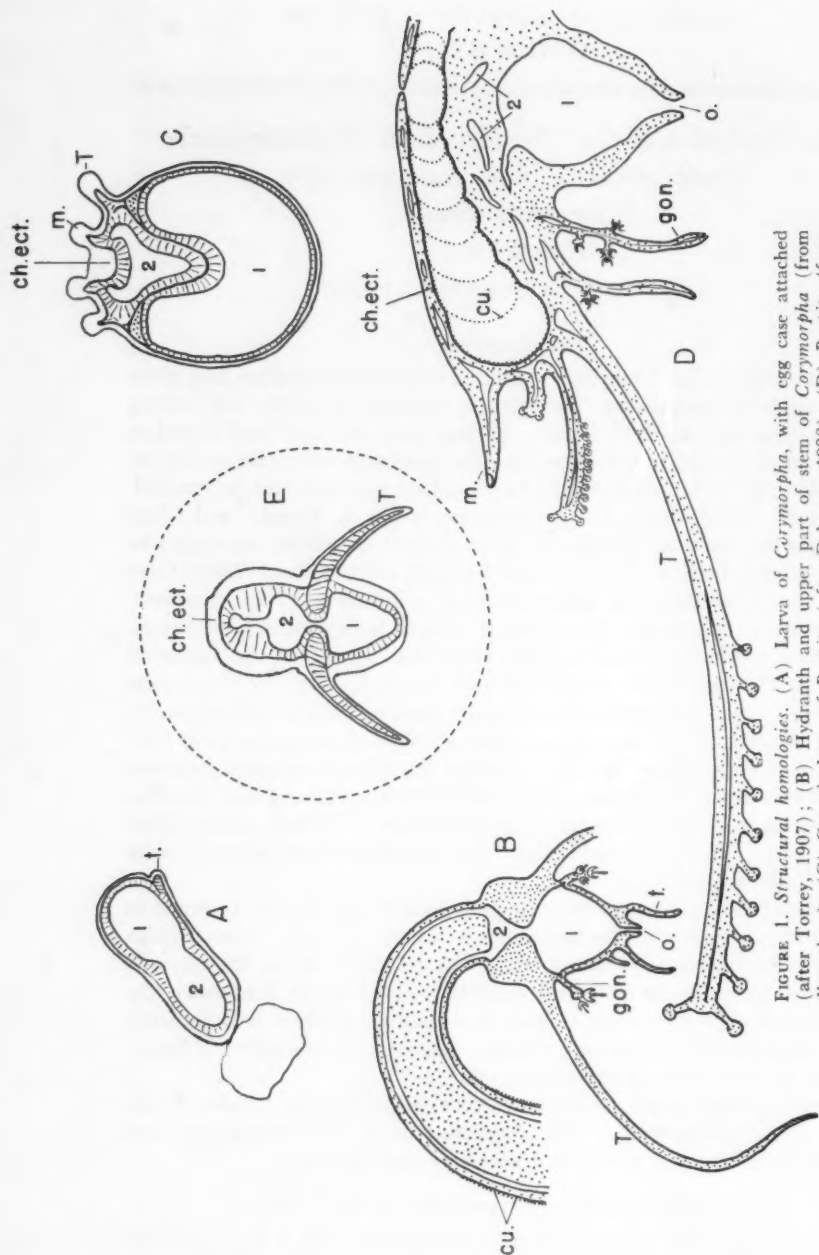
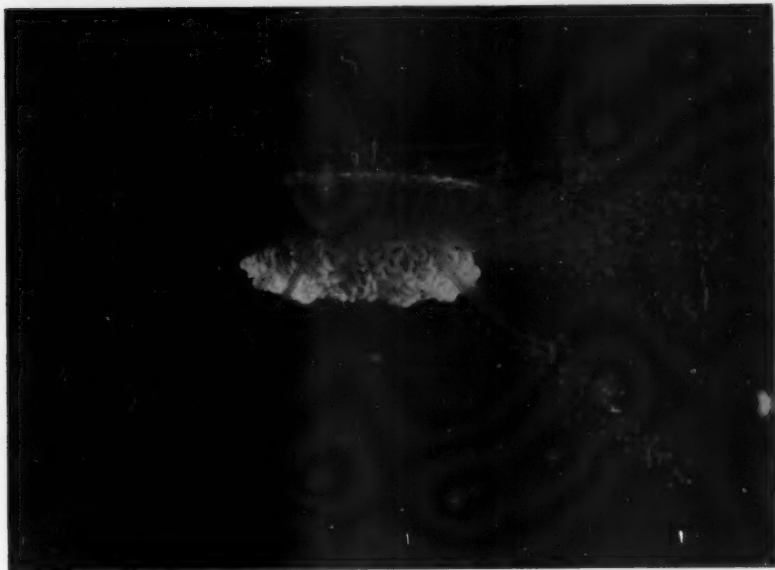


FIGURE 1. Structural homologies. (A) Larva of *Corymophra*, with egg case attached (after Torrey, 1907); (B) Hydranth and upper part of stem of *Corymophra* (from dissections); (C) Conaria larva of *Porpita* (after Delaman, 1923); (D) *Porpita* (from dissections); (E) Actinula larva of *Tubularia* (after Leloup, 1954). *ch. ect.*, chitin-secreting ectoderm; *cu.*, (dotted line) chitinous cuticle in B, float chamber wall in D; *gon.*, structures bearing medusa buds; *m.*, mantle buds; *o.*, mouth of hydranth; *T*, tentacles (proximal tentacles in *Corymophra*); *t.*, distal tentacles; *I*, oral chamber of hydranth; *2*, aboral chamber.

PLATE I. *Porpita porpita* L. (Photo by A. K. Totton)

flap (Fig. 1 D; Fig. 2 *m*) lies flat on the surface. Figure 1 illustrates the morphological homologies between *Porpita* and a sessile hydroid such as *Corymorpha*. The larvae of the two forms are shown in Fig. 1 C and 1 A respectively. Both can be regarded as actinula derivatives. An actinula, that of *Tubularia*, is shown in the centre (Fig. 1 E). While the larva of *Corymorpha* leads only a very short free existence and never shows the typical actinuloid facies, that of *Porpita* is free-living and comparable in fundamental structure to the actinula. This was first shown by Leloup (11) for the conaria larva of *Veleva*, which is similar.

The homologies between the adults will be clear from the illustrations. In the development of *Corymorpha* the aboral region grows out forming the stem, the ectoderm producing a thin cuticle around it. In the development of *Porpita*, this region grows inwards, the ectoderm sinking in and secreting the cuticle as a series of concentric air-filled chambers which form the float. The float is therefore really an invaginated cuticle secreted as a succession of concentric layers like the perisarc of many hydroids.

The mature *Porpita* is a hydranth compressed in its main axis into a wide flat disc, with the aboral region invaginated as a float. If the hydranth is defined as the region from (and including) the proximal tentacles (*T*) to the mouth, then in the mature *Porpita* the mantle flap (*m*), upper part of disc, and invaginated portions can be viewed as stem-counterparts. As will be seen, the mantle flap has a muscular structure and behavioural properties comparable to the stem in *Corymorpha*.

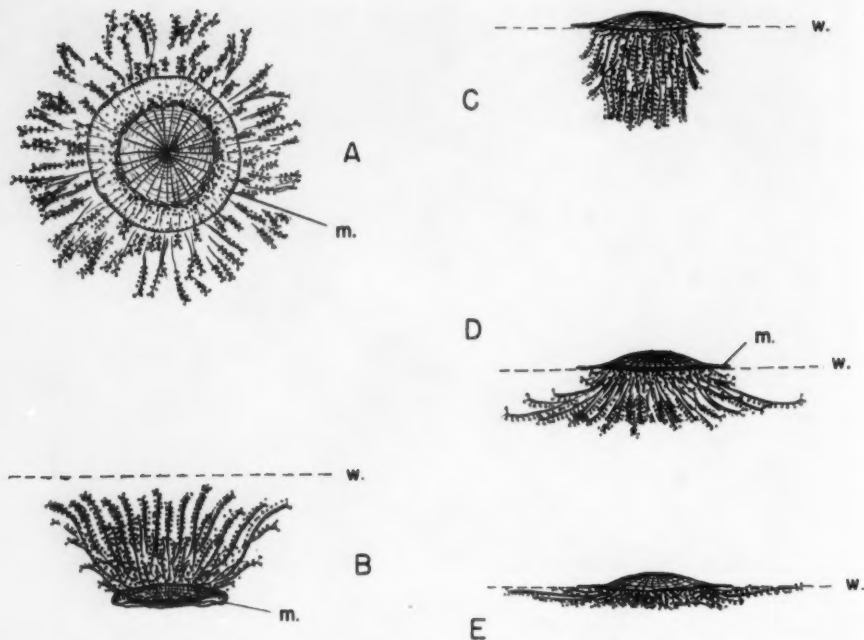


FIGURE 2. *Behaviour* (from photographs and sketches made in the field): (A) *Porpita* in resting position, from above; (B) Righting activity, from the side; (C) Food collecting behaviour, tentacles fully lowered; (D) Resting position, from the side; (E) Aboral, or protective response. *m.*, mantle flap; *w.*, water surface.

The proximal tentacles (*T*) in *Corymorpha* correspond to the tentacles (*T*) in *Porpita*, but in the latter they are budded through life, young and old ones being present in the same animal. Tentacles were seen to undergo autotomy when the animals were treated roughly; this doubtless occurs in natural conditions, the loss being made good by outgrowth and downgrowth of replacements.

The mouth opening (*o*) at the tip of the hydranth of *Corymorpha* corresponds to the opening in the central "zoid" (really the distal part of the hydranth) in *Porpita*. Distal tentacles (*t*) are present in *Corymorpha*, appearing in the early larva; they are not present in *Porpita*.

The structures (*gon*) bearing the medusae in *Corymorpha* find their counterparts in *Porpita*. In the latter they have mouth openings and ingest food (10). Presumably this makes them "zooids"; they are, in fact often referred to as "gonozooids." It would seem, however, that they have acquired individuality secondarily by the process of developing an opening in the tip of what was originally a simple outfolding of the hydranth wall. The existence of the "gonozooids" is the only reason for calling *Porpita* a colonial

coelenterate. The marginal tentacles are no more "dactylozooids" than are those of *Hydra*.

The homologues of the coelenteric cavities are harder to follow. The distal cavity of the hydranth (1) is a large digestive chamber in both cases. The proximal cavity (2) in *Corymorpha* is not represented as such in the adult *Porpita*. In larval development it is broken up into canals by the ingrowth of ectodermal tissue (5). Endoderm canals with frequent anastomoses run in the stem of *Corymorpha* and in the mantle and aboral region (stem homologues) in *Porpita*.

It will be clear, therefore, that there is no trace of "medusoid" organization in a form such as *Porpita*. Further, as Agassiz (1) stressed, the animal resembles a siphonophore less than it does a sessile tubulariid hydroid.

#### MECHANICAL ORGANIZATION

Field observations, dissection, and histological study have been carried out by the author in order to elucidate the mechanics of movement in *Porpita* and *Velella*. The mantle flap, the tentacles, and the organs of ingestion are the only movable parts.

The mantle flap is an outfolding of the body wall which forms a collar around the disc. It is a mobile structure, capable of curling up aborally and of uncurling again into its normal flat position. Radially arranged, unstriated muscle fibres occur in the ectoderm on either side of the mantle. These can be regarded as the homologues of the longitudinal muscle system in the stem of the sessile hydroid. The mantle contains a thick collagenous mesogloea which serves as a support for the muscle fibres. Collagen was identified by the X-ray diffraction technique by Dr. K. M. Rudall, who kindly examined some of the author's material.

The tentacles possess longitudinal muscle fibres in the ectoderm; these fibres are particularly strongly developed in the basal part. The endodermal lining of the tentacles consists of enormous vacuolated cells closely packed together. Cells of this type occur frequently throughout the coelenterates and are known to be skeletal in character, providing a certain stiffness and resilience. The tentacles of *Porpita* do not shorten appreciably when the muscles contract, but bend at their bases. Flexion is in the vertical plane, either towards the mouth or away from it. Lateral movements are slight. The antagonism to muscular contraction in the tentacles evidently resides in the skeletal properties of the endodermal "box-cells." In an anaesthetized specimen, a tentacle can be pressed down or up from its normal resting position but when released it springs back. The more the tentacle is bent, the greater is the resistance and resilience. Endodermal circular muscle is inconspicuous or absent. The box-cells must so reduce the capacity for changes in length that circular muscle cannot play an important part. In *Velella*, by contrast, the box-cells are somewhat smaller, circular muscle is present, and the tentacles (according to Vogt) are in continual movement, writhing and changing in length. The movements of the tentacles in *Porpita* are spas-

modic, sharp, flicking flexions in the vertical plane, with skeletal, not muscular antagonism. The organs of ingestion are mobile, extensible structures with both longitudinal and circular muscle systems. They perform independent, writhing, searching movements.

The distribution of nerves in *Porpita* has been described by Conn and Beyer (4). The system is widespread throughout the ectoderm, but there are no fibre bundles such as occur in the margin of medusae, nor are there any local, ganglionic aggregations of nerve cells. Silver preparations made in the course of the present study show that the fibres are orientated chiefly in the radial direction in the upper side of the disc, becoming more circular round the mantle edge. In *Velella* (14) I have found a double nervous system in the ectoderm, consisting of a system of large fibres which run together forming net-like configurations and an open system of smaller fibres which retain their independence despite frequent close juxtapositions with other fibres. The *Porpita* preparations do not give quite such a clear picture of the relationships between the fibres, but I am confident that the arrangement is essentially the same in the two forms. The "accessory neurons" which I described in my thesis (Oxford, 1956) I now believe to be the counterparts of the open-system fibres in *Velella*. I have not been able to confirm my suggestion that polyploid neurons occur in the *Porpita* nerve net.

#### BEHAVIOURAL STUDIES

The material used in this investigation consisted of specimens collected at Arrecife in the Canary Islands. The animals were recovered from tidal pools following periods of strong onshore wind. Several dozen specimens were examined, and some in apparently perfect condition were transferred to observation tanks in a cool room, where they continued to be active and responsive over the period of study. The specimens were of moderate size, measuring 10–15 mm. across the disc.

##### (a) Vertical Movement

It has been claimed (6; 8) that chondrophores can expel air from the float and so sink below the surface, rising again by resecretion of gases. It is hard to find any first-hand evidence for this. Field observations by Kölliker (10) and Vogt (21) led them to deny that the process took place. The specimens examined in the Canary Islands showed no such tendency, and in the author's opinion, based on histological study, they lack the musculature necessary to expel air in large quantities. In the case of true siphonophores such as *Physophora* the process does, however, definitely occur. It is possible that in the larval chondrophore some such capacity exists, disappearing later (2).

##### (b) Food-Collecting Movements of the Tentacles

The downwards or orally-directed movements of the tentacles in *Porpita* exhibit several degrees of complexity and occur spontaneously as well as in response to tactile stimulation. In an early account Lesson (13) describes

how the movements serve to sweep food particles down into the oral region, where the organs of ingestion pick them up. Observations made in this study also suggest that food-collection is the primary if not the sole purpose of the activity. There appears to be no basis for the statements of some writers that the movements are locomotory. *Porpita* lacks organs of locomotion, drifting passively on the surface. In *Velella*, by contrast, a sail is present. Chun (3) claims that the tentacular movements assist in forcing air out of the stigmata on top of the float, in a sort of breathing process. However, Schneider's experimental investigation (18) of the breathing theory casts serious doubts upon its plausibility. Being at the time of the investigation ignorant of Chun's theory, the present author did not investigate "breathing."

If a tentacle is lightly stimulated by a soft blow from a glass rod, after one or two seconds it will flex a few times in the oral direction, each flexion carrying it a little lower. Unless the stimulus is repeated, the activity dies out after four or five flexions. Each flexion is a sharp jerk. The amplitude, that is, progress achieved by each jerk, decreases the lower the tentacle goes. Presumably this is because skeletal resistance to flexion increases the more the tentacle is bent.

If two or more tentacles are stimulated and respond, their flexions are synchronized whether they are near together or not. The degree of bending, however, is variable. No exceptions to this rule of synchrony were observed.

Small groups of tentacles behave like single tentacles, only a few flexions normally occurring. When a larger number of tentacles is stimulated (how large was not exactly determined) the response takes on a new and distinctive character. All (or nearly all) tentacles, whether stimulated or not, take part and the series of flexions, instead of dying out after four or five, carries on without any outside help for forty or more. The whole response (here called "concerted") has an unmistakable pattern. As with the simple responses, all active tentacles show synchronized flexions (although the degree of depression, and hence the amplitudes of contraction, are not uniform). There is evidently a threshold, to be thought of in terms of numbers of tentacles aroused rather than of strength of stimulation, below which the response is elementary and above which it becomes self-propagating. Once evoked, the concerted response is usually complete. However, in a few instances "false starts" were observed; the concerted response seemed to have begun but failed to develop beyond two or three jerks.

In the experiments the concerted response was usually evoked by bouncing the animal in the water by a light blow on the top of the disc. Mild disturbance of a large enough number of tentacles, whether achieved in this way or by tactile stimulation applied directly to the tentacles sets the response in motion. It was not established whether the "mild disturbance" is effective because it excites touch receptors on the surface of the tentacles or because it bends the tentacles slightly and excites stretch receptors; both may possibly be involved. There is usually a perceptible time lag between stimulus and response, but there is no gradual build-up to the full response; it is concerted

from the outset, the first contraction appearing simultaneously in the whole corps of tentacles (except in the case of "late-starters" mentioned below).

The series of jerking flexions comprising the concerted response has a characteristic pattern. The tentacles are swiftly lowered below the disc (7 contractions in a typical case); they are held there (18 contractions) jerking rapidly (about 200/min.) at very low amplitude. Then decline becomes apparent and the tentacles ascend to the resting position (20 contractions). The jerks usually fade out when the tentacles are about half-way back to the resting position. The three phases of the pattern are really continuous and the number of contractions comprising each phase varies in different performances and between different specimens. Figure 2 D shows the resting position; Fig. 2 C shows the fully lowered position of the tentacles.

The jerking movements evidently represent a conflict between the series of muscular contractions pulling the tentacles downwards and the elasticity of the tentacles resisting flexion and tending to pull them back between flexions. The endodermal box-cells are probably chiefly responsible for these skeletal properties, although the aboral-side musculature might conceivably function passively as elastic tissue. It is unlikely that it is *actively* concerned, because when it does actively contract it produces a much more vigorous type of movement and one which eliminates the concerted, downwards response (see below, p. 16).

In the first part of the cycle, as the tentacles are being brought down, the tempo of contraction increases. As the return takes place it decreases. There appears to be an appropriate frequency (as well as amplitude) of contraction for each degree of inclination. This is evidently related to the varying skeletal resistance. When the tentacle is descending, each muscular jerk encounters greater resistance and achieves less progress than its predecessor. At the same time, the recoil effect in the interval between contractions progressively increases. Thus the accelerating tempo of contraction is adjusted to the increasing strength of recoil: the more powerful the latter becomes, the less time is allowed to it. Downward progress continues in the face of increasing resistance and resilience; it does so not, apparently, because the contractions become stronger but because they become more frequent. When the tentacles are fully lowered resistance is at its maximum. The amount of movement produced by each contraction is so slight, and the frequency of contraction is so high, that the tentacles appear almost motionless. This state of affairs does not last long (four or five seconds). Then the muscular contractions cease to hold their own; the tentacles jerk their way back to the resting position. The contractions are no longer strong enough, or are not of sufficient duration, or are not frequent enough to hold the tentacles down against their own inherent elasticity.

The decline is a gradual one for the further back the tentacles move the weaker become the antagonizing forces. Consequently, there is a progressive lightening of the load on the muscles. The fact that equilibrium is not achieved suggests that the muscular activity continues to weaken right up to

the end despite the lessening of the opposition. By "weakening" is meant simply the lessening in the effects of muscular contraction.

The absolute nature of the synchronization is one of the most striking features of the food-collecting movements. In one specimen, a number of tentacles at one side of the disc seemed unable to achieve the fully lowered position. They beat in a partially depressed position. However, they did not beat at the rate "proper" to their degree of inclination, but showed the rapid tempo of the main group, which were fully depressed. In another specimen a few tentacles were seen to start late in the concerted response. They were motionless until the main group were well down; then they suddenly sprang into life and in two or three rapid, almost continuous flexions reached the position which the main group had achieved only after 6 or 7 flexions.

So far we have dealt with responses to mechanical stimulation. The food-collecting movements may, however, occur spontaneously. Individual tentacles may suddenly become active, without any obvious cause. A more striking type of spontaneous activity also occurs, involving the complete performance of concerted food-collecting cycles at regular intervals. For about five minutes, a typical specimen performed feeding cycles spontaneously at approximately half-minute intervals. The concerted activity lasted about ten seconds, and was followed by about twenty seconds of quiescence. Then, without warning, a new cycle would begin. The concerted performances were identical to those elicited by external stimulation. The regular repetition of the cycles did not endure, but after about five minutes the performances became less frequent, and finally disappeared. The concerted activity could still be evoked experimentally, however. Chun (3) records regular performances of what he believed to be breathing activities, involving movements of the tentacles and other regions. These, he states, occur seldom more than twice a minute. It seems probable that he was observing the same type of activity, although his explanation in terms of breathing is open to doubt.

The spontaneous repetition of the concerted cycles must be regarded as the highest expression of food-collecting behaviour. At the most elementary level we have individual tentacles reacting to local stimulation; then, with two or more tentacles active at the same time we have synchronization of the contractions: then, with a sufficiently widespread stimulus, the response affects all tentacles, whether stimulated or not, and becomes self-propagating through forty or fifty contractions; finally, these concerted performances become self-evoking as well as self-propagating. We have here an illustration of the principle expressed by Pantin (15): "As we go from simpler to more complex behaviour patterns we must always be prepared to find new physiological properties utilized to build up the machinery of behaviour."

Lacking an investigation with physiological equipment one cannot venture a detailed interpretation of these movements on a neuro-muscular basis. The synchronized series of tentacular flexions could be explained theoretically on

a basis of the summation of sensory data arising from stretch-receptors in the tentacles, the sharp resilient backward movement following each contraction causing the stretching. The increasing tempo of contraction as the tentacles descend would thus be linked with the increasing strength (or sharpness) of the resilient recoil movements. The synchronization of tentacular activity indicates that each motor nervous discharge (possibly a single nerve impulse) is through-conducted to all regions. No evidence for decremental spread of impulses was found. The nervous system of *Porpita* would seem to act like a condenser, building up to discharge level by the accumulation of sensory data from all active sources. In spite of the superficial resemblance of the series of step-like contractions to phenomena such as *Calliactis* sphincter closure, it is hard to envisage the mechanism in *Porpita* in terms of facilitation. With regard to the spontaneous outbursts of concerted activity, the absence of localized aggregations of nervous tissue would make it unlikely that a specific pacemaker exists. As in the case of *Arenicola marina* (22) where one of the "pacemakers" is only an ill-defined area of the ventral nerve cord, we may here be dealing with the whole nerve plexus or a large part of it. The term "uncentralized" is so often applied to the coelenterate nervous system that one forgets that it could equally be described as "all-centre."

(c) *Protective Response*

It was explained above that the flexions performed in the oral direction (food-collecting movements) follow mild disturbance or gentle agitation of the tentacles. If a stronger blow is inflicted, or if a tentacle is pinched with forceps a different, though likewise through-conducted, response is evoked. All the tentacles flex in the *aboral* direction. The flexion brings the tentacle tips up to the surface of the water (Fig. 2 E). They are held there stiff and immobile for about two seconds and then the muscles relax.

This reaction has not previously been described and in naming it "protective" the author invokes certain assumptions: (1) that the position of the tentacles flattened against the surface would increase stability and (2) that it would reduce the vulnerability of the animal by presenting to best advantage the armament of nematocysts that are arranged on the knobs along the oral and lateral surfaces. The reaction follows abrupt stimulation such as a predator might inflict.

In no case were partial degrees of response observed. Response follows stimulation without a time lag perceptible to the naked eye. Tentacles remote from the point of stimulation flex in the same moment as the stimulated tentacle. The aboral response is a single sustained flexion, not a series of short jerks. If the stimulus is repeated, the response is sustained for longer.

Administration of a suitably sharp stimulus to an animal engaged in concerted food-collecting behaviour evokes the protective response. The downwards movements are eliminated, and are not resumed following completion of the response.

An interesting phenomenon associated with the aboral response was observed: following the response, the tentacle at which the stimulus had been applied would pass straight through the resting position into a short series of flexions in the oral direction. In experiments on an isolated segment it was found possible to evoke the complete cycle of downwards flexions indirectly by this means (p. 18).

(d) *Righting Behaviour*

Agassiz (1) records the following observations for *Porpita*: "It can, by bringing its tentacles together over the disk, and throwing up the free edge of the mantle in a given direction, then expanding the tentacles of one side far over on the opposite direction beyond the central part of the disk, it can thus readily change the centre of gravity and tilt the disk back again into a normal attitude, should it for any cause have been set afloat with the tentacles uppermost."

Righting behaviour was observed independently in the course of the present study. Overturned specimens embark on a series of unified jerking flexions, of the same type as occur in food-collecting behaviour. Each flexion pushes the tips of the tentacles against the surface of the water, forcing the disc downwards (Fig. 2 B). In the Canary specimens, though not in those studied by Agassiz, flexions were equilateral. Also, the tentacles usually reached equilibrium, jerking to and fro within the  $50^{\circ}$ – $70^{\circ}$  range of inclination from the horizontal. The frequency of contraction in this position was 60–80/min., and the rhythmic beating was sustained for periods over a minute. At the same time as the tentacles are engaged in these movements the mantle flap slowly curls up in the aboral direction. As soon as righting is achieved, the tentacular movements cease and the mantle flap uncurls again, coming to rest parallel to the water surface.

It is clear that the mantle forms a stabilizer when in the extended position. It is normally held flat on the surface, its upper side dry. The curling up which follows overturning would reduce its stabilizing properties, making righting easier. The simultaneous activity of the tentacles would also lessen

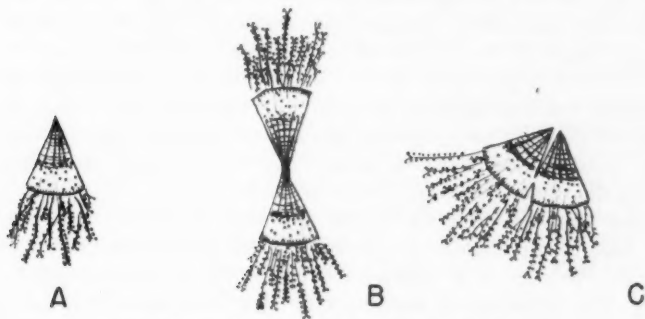


FIGURE 3. *Incision experiments.* Explanation in text.

stability in the inverted position. This was demonstrated to the author's satisfaction by manipulation of righted and overturned specimens in the laboratory.

(e) *Behavioural Results from Incision Experiments*

In Fig. 3 A an isolated 45° segment is shown. In such a piece, concerted food-collecting cycles were obtained by mild tactile stimulation. The protective response was also obtained, but it was followed by concerted feeding behaviour. Small segments were not studied.

Figure 3 B shows two 45° segments connected only by a 4 mm. wide bridge. It was found that movements on either side were co-ordinated. Food-collecting behaviour on both sides could be stopped by a strong stimulus (evoking the protective response) applied to one side.

The 100° fragment shown in Fig. 3 C was incised radially from either side, so that a narrow bridge of tissue was all that connected the two parts. The tentacles in the two halves showed synchronized behaviour. Concerted feeding cycles occurred spontaneously on two occasions in this preparation, the activity beginning at the same moment in the two halves. Thus the behaviour of isolated or partially isolated fragments resembles that of the intact animal.

In order to establish that co-ordination depends on actual tissue continuity and not simply on mechanical contact, a segment was removed from a specimen and its tentacles were thrust in among those of the parent piece. No co-ordination was exhibited between the behaviour of the two portions.

BEHAVIOURAL RESEMBLANCES BETWEEN *CORYMORPHA* AND *PORPITA*

The activities of *Corymorpha* have been studied by a number of workers, the most detailed account being that of Parker (16). Portions of this account are reproduced in his book *The Elementary Nervous System* (17).

The proximal tentacles of *Corymorpha* have an endodermal axis of large vacuolated cells, which Parker refers to as a "plastic skeleton"; following flexion their "elasticity returns the tentacle to its original position," exactly as in *Porpita*. There is longitudinal but not circular muscle in the tentacles. The tentacles respond to mechanical stimulation by flexing in the oral direction. There is a time lag between stimulus and response of "a second or so." In all these respects, *Porpita* is comparable. When kept in quiet water *Corymorpha* exhibits spontaneous food-collecting activities lasting about a minute, with about two minutes quiescence between performances. In *Porpita*, spontaneously repeated activity cycles occur more frequently, but the time ratio of activity to quiescence is similar, viz. 1 : 2.

In these food-collecting cycles, the proximal tentacles of *Corymorpha* exhibit "two or three convulsive efforts," which bring them in around the mouth. In *Porpita*, six or seven such flexions may be necessary for full lowering. The accounts do not explicitly state that the convulsive efforts are synchronous nor that all tentacles take part, but it is implied that such is the case, that is, that the activity is concerted and synchronized, as in

*Porpita*. It would be interesting to find out whether the short series of contractions in *Corymorpha* exhibits acceleration or not, and whether, while the tentacles are being held in around the mouth, they are motionless or are in a state of tetanus, as in *Porpita*.

If a specimen of *Corymorpha* is laid on its side, the stem performs righting movements, bending into a U-shape, and then straightens out as it approaches the upright position. Parker performed experiments showing that the longitudinal muscles of the stem are responsible for these movements, and that the response is a geotropic one. *Porpita* also shows what appears to be a gravity response (in the mantle flap) when overturned. From their location and orientation, the muscles concerned in the two responses can legitimately be viewed as homologous.

Against these resemblances we must place some differences. Nothing comparable to the aboral response of the tentacles in *Porpita* has been described in the proximal tentacles of *Corymorpha*. The distal tentacles (lacking in *Porpita*) take part in food-collecting activity. Bowing movements of the stem also accompany feeding. Most important of all, when a proximal tentacle of *Corymorpha* is stimulated, the response spreads from one tentacle to others with increase in the strength of stimulation. In *Porpita* on the other hand, flexions in the oral direction could be evoked in one tentacle by mild tactile stimulation, but if the stimulus was made sharper the response did not spread to other tentacles; instead, a different response, the aboral one, was called forth.

In spite of their differences it will be seen that the two forms show numerous points of comparison both in the mechanics of movement (for instance, the jerking, orally directed flexions) and in the general character of the behaviour patterns. The spontaneous performance at regular intervals of feeding cycles in both groups is a particularly striking feature. The occurrence of a gravity response in the mantle muscles of *Porpita* and in the homologous aboral musculature of *Corymorpha* shows how a basic functional property can be manifested in widely different ways and yet, on analysis, contribute evidence of relationships.

It may seem at first surprising that the behaviour of the two forms has not diverged to a greater extent. However, the seemingly great differences in habitat and mode of life of the two forms are more apparent than real. We are not dealing with sessile versus free-swimming modes of life. Although *Porpita* moves at the surface of the water it does so passively. It cannot move vertically like a medusa nor alter its spatial relations except by righting itself following overturning. It could be described as sessile with respect to the surface of the water, being attached at the underside of the surface by its float (which is the structural homologue of the stem which attaches *Corymorpha* to the sea floor). It is, in fact, an inverted sessile hydroid with the water surface as its "sea floor." In both *Corymorpha* and *Porpita* there are budded from the hydranth free-swimming medusae which can move vertically in the water and presumably benefit from the dispersal effects of ocean currents different from those encountered by the sessile stage.

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## The New Method of Alpha-Ray Microradiography Applied to the Study of Chick Cartilage

LEONARD F. BÉLANGER, F.R.S.C., AND B. B. MIGICOVSKY

### INTRODUCTION

DEPRIVATION of calcium and vitamin D produces in mammals a general hypertrophy of the epiphyseal cartilage, accompanied by increased metachromatic staining, decreased vascularization, and in extreme cases, cessation of growth (1; 2; 3). The epiphyseal cartilage of birds is even more specialized morphologically. The portion which is the precursor of bone growth (conjugation cartilage; 4) seems the most dramatically affected in the rachitic syndrome (5). Along with concomitant histochemical studies (5; 6), the actual microradiographic observations cast some light on the intimate composition and function of the normal and rachitic epiphyseal cartilage. They also allow a comparison of the effects of various modifying agents.

### MATERIALS AND METHODS

#### *Animals*

The object of this survey has been the tibia of chicks three weeks old and treated as follows:

Group 1: raised from birth on a complete diet (Startena, Ralston).

Group 2: raised on AOAC low Ca-no vitamin D diet (7).

Group 3: raised on AOAC diet, plus vitamin D, 200 units per 100 gms. during the third week.

Group 4: raised on AOAC diet, plus Cortisone (Merck) 25 mg. per 100 gms. during the third week.

Group 5: raised on AOAC diet plus Nilevar (17-ethyl-19-nortestosterone, Searle) 1 gm. per 2 kilos for the third week.

#### *Histology*

The rough dissected bones were fixed for forty-eight hours in a mixture of 1 part neutral formaldehyde and 3 parts 95 per cent ethanol. They were then demineralized in 5 per cent nitric acid in 70 per cent ethanol, dehydrated, embedded in paraffin, and cut mesially along the axis at 10  $\mu$ .

#### *Microradiography*

The paraffin sections were mounted under safelight on celloidin-protected

\*Dedicated to the memory of Pierre Masson, F.R.S.C. Contribution No. 6, Animal Research Institute, Ottawa.

nuclear emulsion (NTA, Eastman), deparaffinized in benzene, and exposed to a 2 mc. polonium<sup>210</sup> source at 26 mm. for twenty-four hours (8). The sections were then detached from the nuclear plate which was developed for five minutes in D 19 (Eastman), then washed quickly in an acetic Stop Bath and fixed for fifteen minutes in Acid Fixer with Hardener (Eastman). The washed and dried microradiographs were finally sealed under coverslips with Permount (Fisher).

## OBSERVATIONS

### 1. *Normal Birds*

The upper extremity of the tibia of three weeks old chicks is a large structure showing macroscopically an articular zone which has a glassy, opalescent appearance in the fresh and which stains predominantly with the acid dyes. Underneath, the conjugation cartilage has a dull, pinkish appearance and it shows a definite preference for the basic dyes. The latter in stained sections consists of two distinct zones: an area of small cells under the articular cartilage and a much wider area where the cells and lacunae are large and more widely dispersed in a matrix which eventually becomes mineralized. Between these two main portions of the conjugation cartilage, a small band of tissue exhibits intense basophilia. In previous experiments (5), it has been revealed as the site of the most intense  $S^{35}O_4$  accretion.

The alpha-ray microradiographs ("alphanradiographs") in the present series have revealed considerable variations in the relative penetration of these different regions of the cartilaginous epiphysis. At the immediate articular surface (Plate I) was a band of high density. Distally, the articular cartilage (Plate I, Fig. 1 zone A), generally of lesser density, showed islands of dense material surrounding blood vessels. The light and dense areas did not have sharp borders but seemed to blend gradually into each other. At the border of the articular and conjugation cartilages there was a band of increased density apparently continuous with the perichondrium (Fig. 1). These observations are related to the intercellular substance. It was interesting to observe that the cells seemed to possess a density different from their immediate environment and could thus easily be recognized as white masses against a dark background or vice versa (Fig. 1).

The zone of small cells of the conjugation cartilage (Fig. 1, zone B) recorded a general low density of the matrix in which denser cells were observed. In the more mature portions these were arranged in linear rows. The narrow band BC could be distinguished as an area of sudden increase of density of both cells and adjacent matrix (Fig. 1, band BC).

Distally, the zone of large cells (Fig. 1, zone C) revealed the presence of dense matrix and cells of progressively lower density. Bone formation was characterized by the sudden appearance of a uniform dense border along cartilage strips invaded by low-density blood vessels in which masses of dense blood cells were irregularly present all the way to the border of the

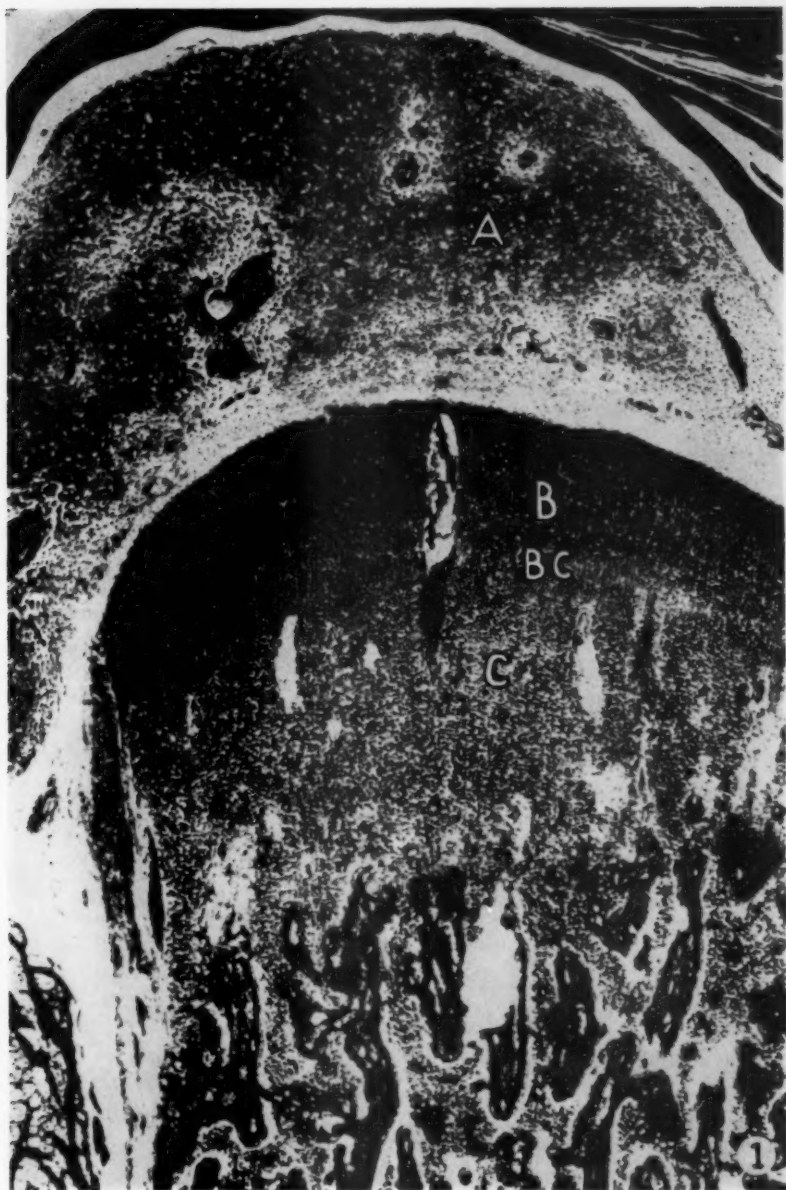


Plate I. FIGURE 1. The upper extremity of the tibia of a three-week-old chick. Alpha-radiograph of a demineralized 10 $\mu$  section,  $\times 50$ . A, articular cartilage; B, zone of small cells; BC, band of maximal  $S^{35}$  uptake; C, zone of large cells.

articular cartilage (Fig. 1). Along the areas of newly formed bone, dense osteoblasts were easily recognized (Fig. 1).

## 2. *Rickets*

The low Ca-no vitamin D diet produced striking changes in "alphanadiographs." The zone of small cells enlarged considerably (Plate II, Fig. 2, zone B), maintaining its normal low density. The zone of large cells, proportionally reduced in size (Fig. 2, zone C), also retained its dense matrix. The band BC disappeared. There were no bone spicules under the cartilage and very few blood vessels had penetrated the matrix. The articular cartilage (Fig. 2, zone A) previously considered unaffected by calcium and vitamin D deprivation (3) was now uniformly clear (except for the epiphyseal centre of bone formation whenever present, as in the lower extremity of the tibia (Fig. 2)). The periosteum, periosteal bone, and the perichondrium remained apparently unchanged.

## 3. *Vitamin D Therapy*

Following a week of vitamin D treatment, the articular cartilage had its normal dense appearance (Fig. 3, zone A); spicules, presumably new, had appeared at the undersurface of the zone of large cells (Fig. 3, zone C), which had grown wider, particularly in the cartilage of the proximal extremity, and had become penetrated again by blood vessels. The most remarkable changes occurred in the zone of small cells. Under a narrow band of low density (Fig. 3, zone B<sub>1</sub>), the matrix acquired high density over a narrow area (Fig. 3, zone B<sub>2</sub>), but this dense band was separated from zone C by a wide band of small cells embedded in low density matrix (Fig. 3, zone B<sub>3</sub>).

## 4. *Cortisone*

The addition of Cortisone to the low Ca-no vitamin D diet did not produce any marked change in the epiphyseal cartilage viewed by alphanadiography (Fig. 4). However, the low density matrix of zone B was penetrated by blood vessels. On the other hand, peripheral bone trabeculae showed evidence of osteoporosis, recognized by localized foci of low density in the older as well as in the recently formed trabeculae.

## 5. *Nilevar*

This anabolic agent produced regional increases in the density of the articular cartilage (Fig. 5, zone A). Within one week it also brought out a large dense zone C, presumably by differentiation of the distal portion of zone B. This area was well penetrated by blood vessels around which compact borders were observed (Fig. 5, zone C). Thick spicules of newly formed bone tissue were present along the distal portion of the cartilage. A large number of dense osteoblasts, osteoclasts, and other elements filled the marrow spaces under the zone of bone growth. The peripheral spicules were numerous and highly alpha-opaque (Fig. 5).

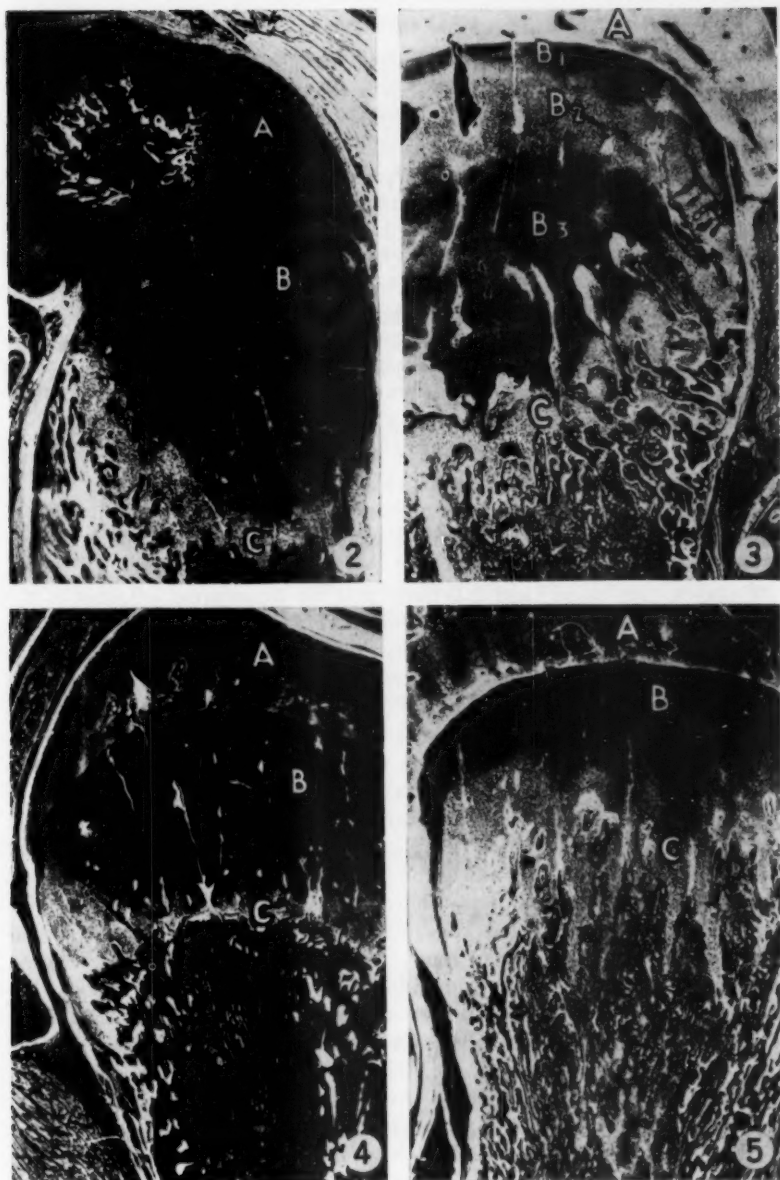


Plate II. FIGURE 2, The lower extremity of the tibia of a three-week-old chick on low Ca-no vitamin D (alfaradiograph as above,  $\times 10$ ); FIGURE 3. Upper extremity, vitamin D treated (alfaradiograph,  $\times 10$ ); FIGURE 4. Upper extremity, low Ca-no vitamin D, plus Cortisone (alfaradiograph,  $\times 10$ ); FIGURE 5. Upper extremity, low Ca-no vitamin D, plus Nilevar (alfaradiograph,  $\times 10$ ).

## DISCUSSION

Some understanding of these microradiographic observations can be obtained in the light of results from a collateral histochemical approach (6) and by comparisons of the present alphasradiographs with previous records of simpler and better understood structures (8).

The image in microradiography represents a gradient of density, whether apparent or masked in the stained section. Thus it has been shown previously that tissues rich in densely arranged filamentous molecules, such as the epidermis, tendons, and muscle fibres, are highly alpha-opaque (8); equally so are cells rich in ergastoplasm and nucleic acids such as those engaged in intense protein synthesis (8), and also cells such as erythrocytes, in which there is a large protein concentration. On the other hand, the ground substance of connective tissue and the product of mucus cells were highly transparent to alpha particles (8).

The ground substance of cartilage contains collagen and mucopolysaccharides (5; 6; 9; 10; 12). Collagen is concentrated at the periphery of the cartilage piece (perichondrium, articular surface) and seems to be responsible for the high density of the alphasradiographs (Figs. 1 to 5) in these locations. In the chick it seems that a special band of collagen finds its way between the articular cartilage and the conjugation cartilage (Fig. 1). "Collagen likes blood" and it is likely that the dense areas adjacent to the blood vessels, within the articular cartilage (Fig. 1) represent concentrations of collagen fibres also. The decrease in the vascularization of the cartilage in rickets (1; 2; 3) might be adverse to the development of collagen so that the low density recorded in rickets would represent a decrease of collagen synthesis. The antiphlogistic effect of Cortisone (11) may also be represented here by anti-collagenism even in the presence of blood vessels (Fig. 4).

On the other hand, the pronounced basophilia of the cartilage matrix previously observed in rickets (5;6) indicates an accumulation of substance which is in great part a mucoprotein, alpha-transparent chondromucoid containing the acid mucopolysaccharide chondroitin sulphate (Fig. 4). In normal cartilage the largest concentration of chondroitin sulphate seems to be in the alpha-transparent zone of small cells (Fig. 1, zone B). On the basis of toluidine blue metachromasia, Sylven (12) has postulated that mineralization is concomitant with a loss of chondroitin sulphate. As a result of our former work involving  $\text{Ca}^{45}$  *in vitro* uptake (5), it also appeared that an early function of vitamin D was to release or destroy the chondroitin sulphate in epiphyseal cartilage, particularly in zone C, presumably by reviving some hydrolytic factor at that level.

The present microradiographic observations have now shown that the changes occurring in zone C do *not* consist in a simple deletion of substance. The sudden increase in the alpha-opacity of the matrix in the zone of large cells (Figs. 1 to 5) is indicative of accretion. As reported elsewhere (6) the

new substance, probably secreted by the large cells, is P.A.S. positive: it is resistant *in vitro* to malt diastase, to hyaluronidase, and to the acids normally used for demineralization. It is hydrolysed by trypsin and papain. Is it collagen again, with a neutral polysaccharide binder between the fibres? The dense material which characterizes bone formation along the distal trabeculae of cartilage is most likely a comparable substance.

What is the effect of the various treatments? Cortisone, a well-known inhibitor of collagen production (11) has not changed the picture of rickets (Figs. 2 and 4) except by causing a loss of ground substance, not noticed appreciably by microradiography.

Vitamin D has undoubtedly stimulated the production of new substance in articular cartilage, in the metaphyseal area of bone formation, and also in the younger portion (Fig. 3, zone B<sub>2</sub>) of the large accumulation of small cells. With time this renewed secretory ability of the conjugation cartilage is extended to the distal area (Fig. 3, zone B<sub>3</sub>). If this change does affect all of the small cells, calcification will occur in two areas (zones B<sub>2</sub> and C) and an island of uncalcified cartilage will be seen between these two zones (10).

The anabolic agent Nilevar evidently has a stimulating effect on cartilage and bone maturation (Fig. 5) and to some extent can be considered as curative of rickets from the histological viewpoint. The present microradiographic survey indicates, however, that the more mature distal cells are primarily affected by Nilevar while the younger cells are stimulated by the vitamin D treatment (Fig. 3).

From a technical viewpoint the present survey demonstrates the accuracy and usefulness of the new method of alphasradiography (8).

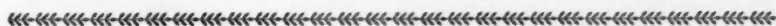
#### ACKNOWLEDGMENTS

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## The Significance of Plant Microfossils Found in Canadian Devonian Rocks

NORMAN W. RADFORTH, F.R.S.C., AND L. WILKINSON

THE manifestation of level of specialization in fossil vascular plants is appreciated largely through an analysis of plant form. Comparative anatomy is often an aid to this end but, in general, fragmentary plant compressions, even with the application of modern palaeobotanical techniques, do not reveal anatomical detail that is diagnostic. This situation confronted William (later Sir William) Dawson when he discovered and described his complex of Gaspé plant compressions which was first assigned to Silurian (2), and which is now considered to be Devonian in age.

These early vascular plants had much in common (on a form basis) with the Scottish Devonian plants in the Rhynie beds. This is recognized through the designation Psilophytales which embraces both groups. Indeed there is basis for the claim that Psilophytinean form was viewed as characterizing Canadian Devonian landscape.

The discovery of other categories of form in Devonian rocks elsewhere and even the appearance in the Australian Silurian of the *Yarravia-Barragwanathia* complex did not alter this view. Indeed, the discovery of more compressions in the Sextant, the Devonian beds south of James Bay offered little to encourage change in this conception.

In an earlier account with Dr. D. C. McGregor (4) the author shared the conclusion that "Spore specialization exceeds in degree that which would apparently obtain from an inspection of the psilophytalean complex, or from other complexes of vascular plants occurring in the Silurian and early Devonian horizons." Thus, for Canada, the suggestion that the degree of specialization as reflected in Psilophytales was surpassed, is supported by microfossil evidence already disclosed. However, the contention has not been examined with reference to macro-micro relationships for a given location. The writers have attempted a first step in this direction by selecting for analysis a single stratum in an exposure of Gaspé Devonian at Tar Point, Gaspé Coast, a collecting site of William Dawson.

### PROCUREMENT OF MATERIAL AND ITS ANALYSIS

It is well known among collectors that at a given collecting site, distribution of macrofossils occurs on two axes, vertical and horizontal. Thus, at a single position where an observer works at an exposure, there are often

several strata which have macrofossils associated with them. These, arranged more or less vertically, are usually separated by barren strata. To the right and left of the observer lateral extensions of the fertile strata occur. Along these extensions fertility often declines or even vanishes though it may recur at a more distant location in the same stratum. The writers deal here with a single stratum at one location in the horizontal plane (for example, see Fig. 1).

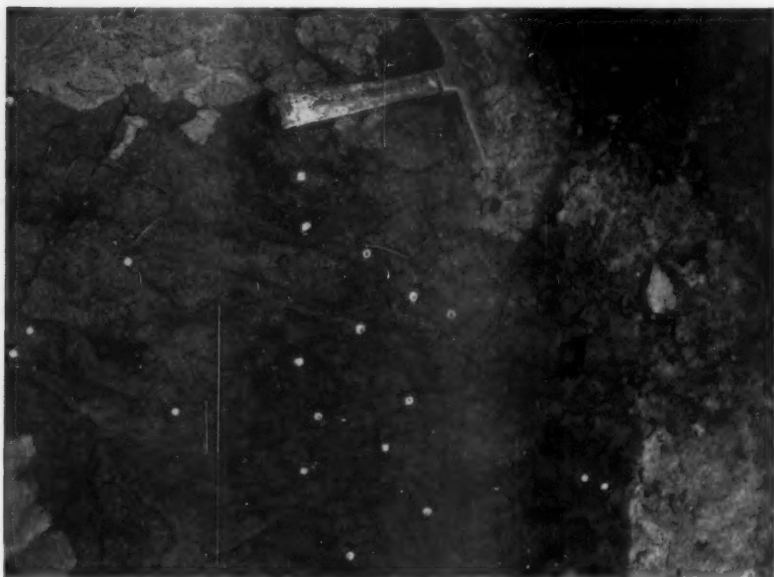


FIGURE 1. Photograph showing macroscopic remains on an exposed stratum *in situ* at Tar Point, Gaspé. White dots indicate presence of compressions.

Pieces of the stratum when removed from *in situ* appear like that shown in Fig. 2, the piece analysed in this work. It is a plate of sandstone with about 100 cm.<sup>2</sup> of the freshly exposed surface shown, covered with a mixture of vegetal remains. In the laboratory a thin layer about 1.5 mm. deep was removed from about two-thirds of this area. This was broken and immediately transferred to a vessel containing hydrofluoric acid. A macerating effect ensued as explained in the method of Radforth and McGregor (4). The organic residue from this treatment was then treated with Schultze's solution and particles in the residue were rendered semi-transparent.

Though procurement of coarse fragments was not essential for this investigation it was thought that had they not been cleared, disclosure of

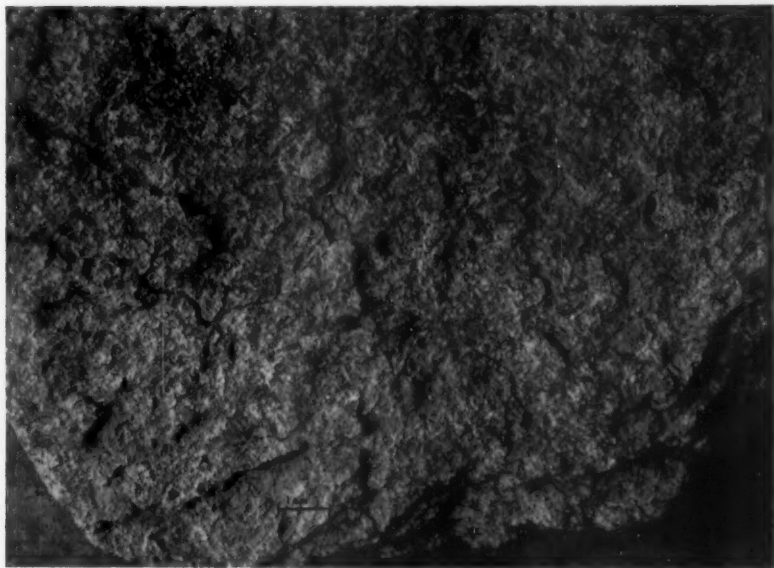


FIGURE 2. Freshly prepared surface of rock shown in Fig. 1 from which a lamina was removed for maceration.

microfossils might have been incomplete owing to obscuring effect in the mounts. Mounts of the residue were made by pipetting two drops onto slides onto which 60 per cent corn syrup had been applied as the mounting medium (*cf.* 4).

#### OBSERVATIONS AND CONCLUSIONS

Mounts of the residue were found to contain several kinds of microfossils in sufficiently large numbers to permit determination of relative frequency. However, for this report the writers emphasize morphological range, not quantity representation. Examples of the kinds procured are represented in Plate I, Figs. 1-15. It should be indicated that all microfossils shown are from a lamina of rock bearing a single superficial compression mixture exposed from a single stratum. Also, only those kinds which together demonstrate maximum form range are figured.

The fragments of macroscopic size appearing on the lamina and in the mounts following maceration cannot as yet be identified according to genus. However, the claim may be made that no fragments other than those of Psilophytalean origin were observed, and that probably only one species was represented.

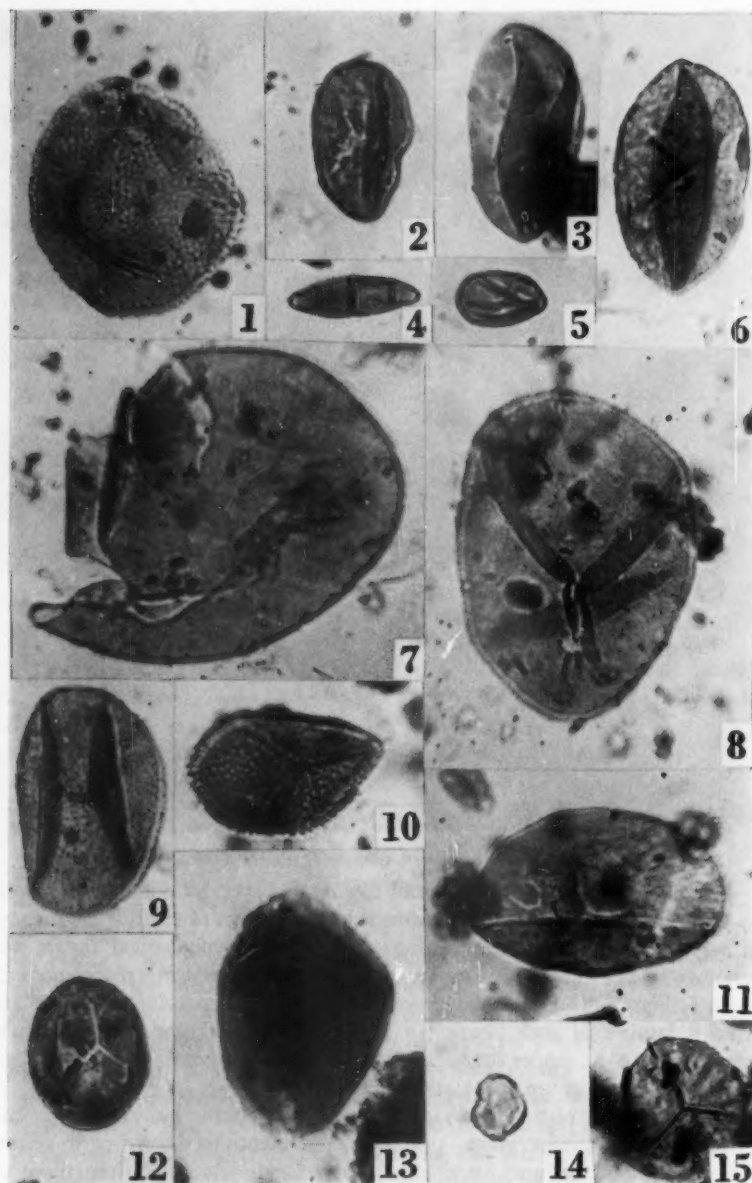


PLATE I, FIGURES 1-15. A conspectus of microfossils from a single lamina (cf. Fig. 2) showing range in complexity. Approximately eight different kinds of specialization suggest themselves (Scale: 1cm. = 20 $\mu$ ).

## DISCUSSION

The reader may tend to reconcile the macrofossil assemblage, represented here by a single taxon, with that procured by Dawson for Tar Point, and which numbers two genera (*Psilophyton* and *Arthrostroma*) (1). This would be difficult because it involves comparison of sources of material which are not equivalent; one being from a single lamina of one stratum, the others from many strata geographically and historically separated. Thus, the macrofossil component in the present work has its own local significance, and is in fact only an element of the larger assemblage of Dawson.

A more reasonable contrast arises when the microfossil assemblage is considered with either the equivalent macrofossil element or that of more extensive geological and geographical origin. The microfossils suggest the presence of more kinds of plants than do macrofossil sources.

Further comparison of the two sources of plant material suggests that whereas for the microfossils at least eight features of divergent specialization are observable<sup>1</sup> no major diagnostic feature can be suggested to separate the macroscopic remains into species, and therefore, on this basis, comparatively no specialization is indicated among the latter. To appreciate this fully, it must be recalled that where morphological peculiarity exists in the exospore or exine of a microfossil, the condition usually implies natural species or variety categorization for the plant in which the microfossil originated. On occasion, experience has shown that an isolated spore can be an immature one which, because of this, will possess a pattern different from that of a mature example of the same species (3). However, unless the spore is very young, in which case it is likely to be attached to its original mass, the difference noted is one of degree, and its natural taxonomic categorization can be recognized. The microfossils of Tar Point (Plate I, Figs. 1-15) on the other hand, evidently show differences in pattern which arise from differences in biological trend. This supports the contention of species separation and therefore, to that degree, range in specialization.

There is double inference in acknowledgment of the wide range of specialization in the microfossils. The living components of Devonian landscape were certainly more numerous and probably far more complex than the macrofossil assemblage signifies. The fact that this situation is reflected from the study of a few square inches of Devonian terrain strikingly emphasizes the high probability of this claim.

It seems very important to avoid arbitrary action in claiming a major feature of specialization in a microfossil, especially if such a feature is to mark the establishment of a biological trend in the species that the microfossil represents. Also, a well-delineated feature could be simple or compound, and in a given microfossil could be shared with one or more marked features which in their turn could be simple or compound. This makes for

<sup>1</sup>Cf. Trans. Roy. Soc. Canada, Series III, vol. L, Sec. V, Plate II, p. 31, and this paper, Plate I, Figs. 1-15.

difficulty in arranging an acceptable basis for agreement on what features are the fundamental natural marks of specialization.

On the other hand, a number of observers have no difficulty in deciding which microfossils in an assemblage are the most elaborate. Moreover, they can agree when, on the basis of elaborations, microfossils are specifically different. Thus, if a smooth, thin-walled spherical spore is regarded as the simplest all others that differ from it in shape, pattern, or thickness of wall or in a combination of these are more elaborate. If, among these, elaboration is reflected differently in each one of the complex, it would seem reasonable to regard that assemblage as demonstrating maximum complexity or specialization for the assemblage.

Now that it is known that microfossils in the Tar Point sample occur and can be disclosed in significant number exhibiting broad specialization, statistical study with reference to specialization will be attempted for this and other fertile strata in the series.

It seems worth noting that the range of specialization is not only a reflection of phylogenetic trend or circumstance but also an index pertaining to specific environment. One might claim with some justification that the assemblage, being derived as it is from a single lamina, is the equivalent of a given level in an unconsolidated sedimentary sequence such as those found in Pleistocene deposits. Its range of specialization enables the observer to appreciate habitat composition and complexity for the time when the lamina was formed. Also, it serves as an index to sedimentary identity and, when used in contrast with those for other places in the stratum, might lead to an understanding of local sedimentary ontogeny.

It may be of interest to mention that the writers think that application of nomenclature to work of this nature is not essential. In fact the investigator, by avoiding nomenclatural problems, is more likely to count a single biological trend as reflected in, say, spore pattern as one natural entity, whereas taxonomic history with its attendant peculiarities in micropalaeobotany may have artificially applied two names (or more) to one trend.

#### ACKNOWLEDGMENT

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## Definitive Microfossils Pertinent to Physiographic Difference in Muskeg

NORMAN W. RADFORTH, F.R.S.C., AND LYNDIA S. SUGUITAN

IT was indicated in earlier work by the author (2; 3) that muskeg, now defined as organic terrain, varies in fundamentally consistent ways, and that these variations are revealed in the plant cover. Such cover occurs frequently in small areas of the terrain which are known as bogs when contained in a local pocket of land. It is even more general when the organic terrain is continuous, the common condition in the Hudson Bay lowlands, the Northwest Territories, and the Yukon. The phenomenon has aided in the development of a basis of reference in classification for ground level and aerial interpretation of organic terrain (4).

Sjörs writes of the occurrence of different kinds of muskeg (7), but in his account he states that "Some types of pattern recur frequently, but on the whole the patterns are dissimilar and cannot be easily classified into a system of forms of more than local validity." If inconsistency of type is real, it renders classification difficult, especially if such inconsistency is frequent and cannot be explained.

The authors now turn to the problem of examining a basis for explanation. Inconsistency had to be assumed on the basis of indecision experienced when field categorization of a selected example of organic terrain was attempted.

### TERRAIN ANALYSIS

A muskeg location near Copetown, Ontario, was chosen as an example because of its apparent similarity with another known to exist near Fort Churchill, Manitoba, where organic terrain is relatively common. The general area (Fig. 1) possesses representative cover formulae (cf. 2). In one or two portions of the total area it was difficult to assign areas exceeding 100 sq. metres to a major category. If FI (e.g., eriophoroid-moss) is selected as the cover formula there is hesitancy because of the occurrence of EI (e.g., ericoid-moss) in some places. In neighbouring areas, if EI appears to predominate, marked occurrence of FI is noted. Hence, there was general indecision when attempts were made to assign the whole area to one recognized category of muskeg.

Air-form classification of this kind of terrain is not so difficult. Examples of it are usually designated "dermatoid" (6). If the distribution of EI is such that it occurs in islands as large as 25 sq. metres, the terrain would then be classed as "terrazoid." However, difficulty arises with interpretation in



FIGURE 1. Photograph showing cover type admixture (FI and EI) on the Copetown bog.

that, in the course of interpretive method, unless topographic qualification can be ascertained, homogeneity of sub-surface structure may be assumed by the interpreter. In fact, it has not been established whether homogeneity or heterogeneity obtains. Thus, vegetal history is uncertain for this kind of organic terrain and in these circumstances there would be hesitancy in predicting fundamental physiographic characteristics. If a moderate degree of heterogeneity were to exist, would it be a constant feature?

The authors attempted microfossil analysis at Copetown and Fort Churchill locations with the hope of revealing primary organization in these circumstances. Three series of borings from apparently delineated areas were compared. The first and second series comprised two borings each, and both series were from Copetown. The first series was taken in a pure FI zone and the second in a zone where EI invaded in the form of patches, sometimes so small as to appear as mounds measuring about a third of a metre at their bases.

For the Fort Churchill location only one boring (V) was examined but to provide a basis for comparison, consideration of analysis made earlier (VI) has been given. These two borings for the Fort Churchill area, though widely separated, are for the same topographic and vegetal coverage classification. The cover formula is FI for each case, but EI is close enough to contribute to the kind of indecision that has apparently arisen with reference to the examples from the Copetown area.

At depth increments of 2.5 cms., the peat in each of the five borings was examined for pollen and spore microfossils. Slides of corn syrup mounts, the preparations required for this, were obtained using a method described elsewhere (1). From the mounts, and for every depth increment, 150 grains or spores were identified and counted at random. Totals for each microfossil type were then expressed in per cent relative to the over-all total of 150.

### RESULTS

The results are expressed in Table I. In recording them no attempt has been made to account for sources of error. Considerations in the literature suggest that where error occurs, it does so to the same degree, for all practical purposes, for all cases analysed. Thus, if comparison of results is anticipated, the effect of error is cancelled provided, of course, the interpretive procedure is appropriate. Because the authors feel that the interpretive procedure is appropriate in the present work, and because the question of error has been dealt with adequately elsewhere (8, p. 49), no analysis of it will be made here.

It might also be claimed that mistakes in identification are possible, and that photographs of the kinds of microfossils named should appear in the text. As is the case with possible sources of error, however, the practice is that identification is accepted, and unless some particular aspect of diagnosis is in question photographs or drawings are not deemed necessary.

### DISCUSSION AND CONCLUSIONS

In cases where EI has persisted as reflected by unquestionable predominance in the ground cover, and as indicated by the gross structure of the peat beneath, it is almost invariably the case that the predominating microfossils are those with index units VII and X, Ericaceae and Sphagnaceae respectively (5, cf. Fig. 18, p. 64, depths 0–20 inches). This condition arises when EI is widespread and in continuous muskeg. Also, though index unit IX, Cyperaceae, is in evidence in these conditions it lacks the relative prominence of VII and X.

The situation in the Copetown Bog (Table I, series 1 and 2) demonstrates approximately equal prominence for VII and IX. The degree of difference, if present, favours neither unit consistently. Note, however, that although range of prominence of IX in both series at Copetown is lower than it is for both FI series of Fort Churchill it is considerably higher than that for VII at Fort Churchill. Also, it is higher than it is for muskeg where EI is consistently prominent.

Thus, because IX is prominent for both kinds of cover at Copetown in spite of EI prominence in series 2 (EI, Table I) there is a reasonable argument that the Copetown Bog might be classed as constructed basically according to an FI trend as to its subsurface constitution. The reasonableness of this claim is appreciated all the more where reference is made to a condition where EI and FI are widespread (3, pp. 62, 64, 65). It is of practical as well as of academic interest to note that to derive the basic information leading to these conclusions only about 10 cm. of core is required.

Once the microfossil determinations have been made, the relationship of the results to physiographic circumstances can be assessed. This is facilitated by the fact that where index unit number IX occurs at the expense of index units VII and X, or has generally equal prominence, the habitat is invariably wetter. This implies the presence under these conditions of a depression type

TABLE I

THE COMPARATIVE DATA (MICROFOSSIL FREQUENCIES PER CENT) FOR BORINGS MADE FROM AREAS AT COPETOWN, ONTARIO, AND FORT CHURCHILL, MANITOBA, FOR WHICH INDICATION WAS EXPERIENCED BECAUSE OF AMBIGUITY OF COVER TYPES

| Location of Muskeg           |  | Cape Town, Ontario |  |  |  |  |                  |  |  |  |  | Ft. Churchill, Manitoba |  |  |  |  |                  |  |  |  |  |                  |  |  |  |  |                  |  |  |  |  |                  |  |  |  |  |
|------------------------------|--|--------------------|--|--|--|--|------------------|--|--|--|--|-------------------------|--|--|--|--|------------------|--|--|--|--|------------------|--|--|--|--|------------------|--|--|--|--|------------------|--|--|--|--|
| Series no. and Cover Formula |  | 1, FI              |  |  |  |  | 2, EI            |  |  |  |  | 3, FI                   |  |  |  |  |                  |  |  |  |  |                  |  |  |  |  |                  |  |  |  |  |                  |  |  |  |  |
| Bore No.                     |  | I                  |  |  |  |  | II               |  |  |  |  | III                     |  |  |  |  | IV               |  |  |  |  | V                |  |  |  |  | VI               |  |  |  |  |                  |  |  |  |  |
| Increment                    |  | 2.5 5.0 7.5 10.0   |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0        |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  |
| Depth (cm)                   |  | 2.5 5.0 7.5 10.0   |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0        |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  |
| Microfossil                  |  | 2.5 5.0 7.5 10.0   |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0        |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  |
| Index No.                    |  | 2.5 5.0 7.5 10.0   |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0        |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  |
| Kind                         |  | 2.5 5.0 7.5 10.0   |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0        |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  |
|                              |  | 2.5 5.0 7.5 10.0   |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0        |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  |
|                              |  | 2.5 5.0 7.5 10.0   |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0        |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  |
|                              |  | 2.5 5.0 7.5 10.0   |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0        |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  |
|                              |  | 2.5 5.0 7.5 10.0   |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0        |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  |
|                              |  | 2.5 5.0 7.5 10.0   |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0        |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  |
|                              |  | 2.5 5.0 7.5 10.0   |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0        |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  |
|                              |  | 2.5 5.0 7.5 10.0   |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0        |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  |
|                              |  | 2.5 5.0 7.5 10.0   |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0        |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  |
|                              |  | 2.5 5.0 7.5 10.0   |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0        |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  |
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|                              |  | 2.5 5.0 7.5 10.0   |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0        |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  |
|                              |  | 2.5 5.0 7.5 10.0   |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0        |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  | 2.5 5.0 7.5 10.0 |  |  |  |  |
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of land form. The shape of the depression is, of course, another matter. It depends on whether or not the origin of the depression is due to primary or secondary reasons. If the former, then contour of the mineral sub-layer will be of direct significance. If the latter, then the local hydrological circumstances will be more important. Sometimes the secondary effect is accountable to man or to an animal which selects the habitat and changes the drainage pattern to suit its own requirements. In North America the beaver is an example of this kind of agent. In European countries or in eastern Canada where peat mining is an industry, wide trenching or ditching invariably results in rehabilitation of FI cover. Under natural conditions secondary drainage pattern is sometimes induced because of naturally increased elevation of the organic terrain adjacent to the area in question. Where this condition arises it does not result in the rehabilitation of the surface cover to FI; rather it insures the maintenance of the FI type of cover which already exists.

Under these natural conditions of change, the shape of the depression will obviously be controlled by the disposition of the local elevation. Sometimes a wide channel is formed which is completely covered by the indecisive mixture of FI and EI. In these circumstances, the EI is often distributed in such a way as to form characteristic ridges which produce a reticuloid pattern when viewed from the air. Because of this, by reason of the mechanics of classification, the area is no longer in the indecisive category. There are cases where the shape of the depression is funnel-like and sometimes there is open water visible at the neck of the "funnel." This too is recognizable by the reticuloid pattern and becomes the decisive rather than the indecisive state by reason of the application of taxonomic method.

Sometimes an apparently indecisive condition occurs where mounding is erratic and widespread. In these circumstances the physiographic conditions usually suggest the presence of a shallow basin of peat with shallow gradient at the margins, enclosed by a large expanse of organic terrain generally. Where the environmental physiography is such that mineral outcrops appear abruptly, the basin may be very deep. There are cases, of course, where the condition is basically primary but with a secondary effect at the margins of the conformation. In these cases there will probably be convolutions at the margins of the depression.

Turning to vegetal considerations, the mixed condition of EI and FI requires some examination with reference to the principle of succession. Table I, series 1 and 2, suggests that the ericaceous and sphagnaceous factors have been competing to some degree, at least for the time it took to accumulate a depth of 10 cm. of fossilized remains. Neither factor, however, appears to have become predominant at any stage. Indeed this situation is reflected in the present cover. Thus the condition provides a strong argument supporting a view that the mixture represents a kind of self-sustaining climax, with eriophoraceous members as a fundamental component. Whatever the interpretation concerning the vegetal state, it would seem clear that the ericaceous-sphagnaceous component does not suggest invasion, or com-

petition would result in the area being brought under the domination of ericoids, which would in turn encourage prediction of a shrub or tree layer for the future.

The condition of stability reflected in the history of the vegetation, leads to a theoretical conclusion with regard to physiographic circumstances. If the FI condition has been persistently maintained, a relatively high degree of wetness has always prevailed wherever the circumstances are primary. Thus, if on the basis of topographic study the primary and the secondary conditions can be separated and the primary assigned, the mixed condition designates the contour of the low point of the drainage gradient that has existed since the withdrawal of the last components of the last glacier. In the Copetown area there is no evidence of the presence of any topographic feature that would render the area under investigation a feature of secondary drainage. Superficial examination of the area does not reveal a drainage course near the outside of the bog where the indecisive cover condition is to be found. There are several areas of open water which are not always obvious because of the overgrowing vegetal cover. However, if the indecisive mixture of vegetal cover is traced, its direction is such that it links these infrequent small pond-like areas. There is a direction of movement of the water in them and this also follows the direction of the mixed cover type. Thus the mixed cover type must be regarded as an indicator, not only of the relative low point in drainage gradient, but also of where the gradient is low in range, that range being delineated by the presence of the mixed cover formula.

In the Fort Churchill area, drainage results in frequent impounding. Open and closed ponds alike are usually associated with climax recognized here and suggest the low point in drainage gradient. Where there are open ponds in groups these suggest the major drainage depressions to which flow is directed wherever there is free water percolating through the peat.

There would seem to be two major applications of the results of these investigations. One is that the apparent indecisiveness that the presence of mixed cover formulae encourages need not obtain if knowledge of the sub-surface constitution of the peat is required, for this is the same as it is for the FI condition and the peat category will be decisive. The other is that presence of these particular mixed cover formulae indicates characteristic physiographic contour which can now be determined relatively easily according to the reasoning developed in this account. It is, of course, appreciated that these two applications are more obvious wherever aerial survey is possible.

Difficulty of delineation will undoubtedly arise with respect to other major classified types of air-form and ground-form patterns for organic terrain. When such cases are revealed and the analytical data for them is known, aerial interpretation of organic terrain will lead directly to more exact knowledge of sub-surface structural and topographic conditions which is so important for programmes of development for the north.

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